REGENERATION OF THE PROBOSCIS, RADULA AND ODONTOPHORAL CARTILAGE OF THE SOUTHERN OYSTER DRILL *THAIS HAEMASTOMA CANALICULATA* (GRAY) (PROSOBRANCHIA: MURICIDAE) AFTER AMPUTATION

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ABSTRACT

The ability of *Thais haemastoma canaliculata* (Gray) to regenerate a fully functional proboscis, radula, odontophore, and radular sac after complete amputation of all structures was investigated. All drills from which the radular mechanism was removed, completely recovered from the anesthesia and surgery and were actively moving about the tank within one day post amputation. Snails resumed feeding only after the entire radular mechanism was completely regenerated. The entire regenerative process occurred within four to five weeks post-amputation. These drills exhibited normal feeding behavior and produced normal boreholes in oyster shells. The regenerated radula and its accessory structures were normal in appearance and closely resembled original structures except for size; the regenerated structures were slightly smaller in size than their original complements.

Muricid gastropods possess the ability to regenerate lost organs. Regeneration of the proboscis and radula has been studied in several species of muricids (Demoran and Gunter, 1956; Carriker et al., 1972). Carriker et al. (1972) conducted a comprehensive investigation of the ability of *Urosalpinx cinerea* (Say) and *Eupleura caudata etterea* Baker to regenerate their proboscis after amputation. These snails were capable of regenerating both the radula and proboscis. Demoran and Gunter (1956) reported the same regenerative ability in the southern oyster drill *Thais haemastoma* (Lamarck); however, in their short note they mentioned no qualitative or quantitative observations of the regenerated proboscis and radula as compared to the original structures. There is a paucity of information concerning regenerative ability in *Thais* sp. after extensive damage to the proboscis (i.e., complete amputation of radula, odontophore, and radular sac).

The objectives of this investigation were to (1) observe the structure of the radula of *T. haemastoma canaliculata* (Gray) (Abbott, 1974) using scanning electron microscopy; (2) determine if the proboscis, radula, and odontophoral cartilage will regenerate after complete amputation of these structures; (3) observe morphological differences between original and regenerated structures; (4) determine the time interval necessary for complete regeneration of these structures; and (5) determine the time when post-amputation feeding by the snails resumes.

MATERIALS AND METHODS

Seventy adult oyster drills (mean shell length = 61.6 mm) were collected at Grand Isle, Louisiana, U.S.A. The snails were transported to the laboratory and placed into two 38 L aquaria at room temperature (23–25°C and 20‰ salinity (Instant Ocean® Sea Water Mix). Fifty snails (male:female = 1:1) were placed in one aquarium (tank A) to be used in the determination of the time and extent of regeneration of the proboscis. Plexiglas dividers were used in the second aquarium (tank B) to separate the remaining 20 snails (one snail/chamber) that were used to determine the post-probosectomy time at which feeding would resume. The male-to-female ratio in tank B was also 1:1. Both tanks were aerated throughout the experiment. The snails were allowed two weeks to acclimate to the laboratory conditions before the experiment began. Oysters (*Crassostrea virginica* [Gmelin]) and clams (*Rangia cuneata* [Sowerby]) were pro-

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vided as prey during the acclimation period. Empty oyster shells from tank B were saved for a scanning electron microscopy (SEM) investigation of bore holes.

Magnesium sulfate was not an effective narcotizing agent for *T. haemastoma canaliculata* in that it took a high concentration of the substance to anesthetize the snails and also required an extensive period of time to take effect. More importantly, the snails did not protrude their proboscides under $MgSO_4$ treatment, which was required for a complete amputation. Sevin® dust (1-napthyl-N-methylcarbamate) was finally chosen as an appropriate anesthetic agent (Carriker and Blake, 1959). Snails were placed in 3 L of a 1 ppm solution of Sevin® in 20°/ooS sea water. Sevin® was first dissolved in a minimal amount (15 ml) of acetone before mixing with sea water. Approximately one hour was required for complete anesthetization. Drills were considered completely anesthetized (Fig. 1) when they fully extended their proboscis for more than half of their body length. The proboscis of each snail was pulled gently with a pair of fine forceps to further extend it and was then amputated at its base with a pair of iris scissors. Each proboscis was prepared for either SEM or light microscopy. All proboscides were examined after amputation to insure complete removal of all radular structures. After probosectomy, each drill was returned to its tank where full recovery from anesthesia occurred within two days. The snails were considered recovered when actively moving about. There were no observable effects from the anesthesia.

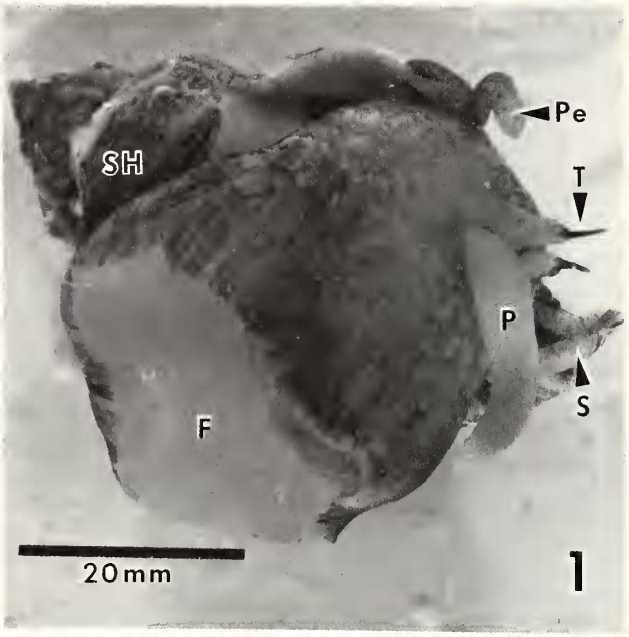
After drills completely recovered from anesthesia, live oysters were placed in both tanks. Oysters were examined daily for any evidence of predation and were regularly replaced with fresh oysters.

Five snails were sacrificed from tank A per week for ten weeks and examined for evidence of regeneration. All regenerated material was preserved for later histological examination. The sex of each snail was also determined at that time.

When an oyster from tank B showed evidence of snail predation (bore holes; Fig. 2), it was removed from the tank and the number of the snail feeding upon it was recorded. Snails from tank B that had preyed upon oysters were sacrificed and their regenerated proboscides were prepared for microscopical examination.

For SEM the original and regenerated proboscides of drills were dissected by making a longitudinal cut through the dorsal epithelium and muscle layers to expose the radulae and odontophores. The tissues were fixed overnight with 2.5% gluteraldehyde in 0.2M sodium cacodylate-sucrose buffer (585 mOsm; pH = 8.0). Specimens were rinsed for 1 h in three changes of distilled water to remove all buffer salts, dehydrated in acidified 2,2-dimethoxypropane, critical-point dried in CO_2, and sputter-coated with 200Å of gold-palladium. Specimens were then examined with a Hitachi S-500 SEM at 25 KV.

Oyster shells from tank B were prepared for SEM study by air drying followed by critical-point drying in CO_2. Shells were then sputter-coated with 200Å of gold-paladium.



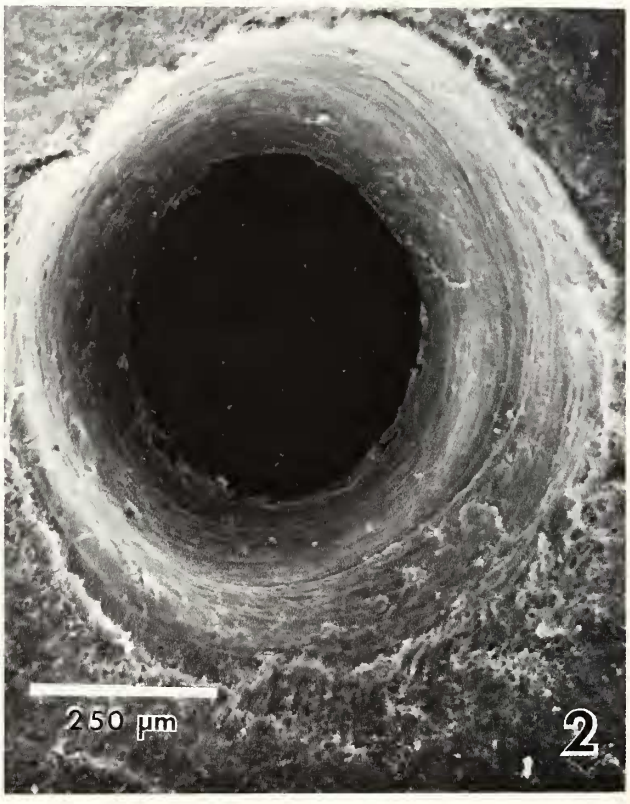


Fig. 1. Anesthetized oyster drill, *(Thais haemastoma canaliculata)* after 1 h in 1 ppm Sevin®; F = foot; P = extended proboscis; Pe = penis; S = siphon; SH = Shell; T = tentacles. **Fig. 2.** Borehole in shell of oyster *Crassostrea virginica* made by snail in Fig. 1.

For light microscopy the proboscis of each drill was fixed in formalin-acetic acid-alcohol (FAA) overnight, dehydrated in ethanol, cleared in xylene, and embedded in paraffin. Sections (10 μm) were stained with azan (Humason, 1972).

The following measurements (Fig. 3) were made on original and regenerated radulae of ten snails: mean radular width, mean radular length, mean total width of rachidial teeth, mean length/width of central rachidial cusp, mean width of individual lateral cusp, and mean odontophore width. Differences between original and regenerated radulae were compared by a paired t-test.

RESULTS

The radular and odontophoral cartilage of *Thais haemastoma canaliculata* lies within a long, muscular sheath known as the proboscis (Fig. 1). The proboscis and radula of *T. haemastoma* are very similar to those of *Urosalpinx cinerea* described by Carriker (1943). The proboscis (Figs. 4,5,6) is composed of an outer thick layer of circular muscle surrounding two inner layers of oblique muscle. Lining the lumen of the proboscis is a thick layer of longitudinal muscle. The proboscis sheath is covered by a mucous-secreting epithelium containing many goblet-type cells. The proboscis contains myoglobin giving the distal end a reddish appearance. The radular and odontophoral cartilage (Figs. 8,10,11) lies within the distal one-third of the proboscis with many associated nerves and muscles for the protrusion and retraction. The radula of *T. haemastoma* like that of *U. cinerea* (Carriker, 1943; Carriker et al., 1972) is of the rachiglossan type (Fretter and Graham, 1962) and is composed of three rows of longitudinal teeth: a central row of five-cusped, rachidial teeth and two lateral rows of single-cusped, marginal teeth (Fig. 9). The radula lies on the radular membrane that covers the odontophoral cartilage (Figs. 8,11). The proximal portion of the radula is enclosed within a radular sac that curves 180° distally and is attached by muscles to the proximal base of the odontophore (Figs. 8,10). The radular teeth of *T. haemastoma*, like those of most oyster drills (Carriker, 1943 et al. 1972; Fretter and Graham, 1962) point "backwards" or proximally (Figs. 8,9,11). The radula is protruded out of the proboscis, placed against the substratum or food to be scraped, and then retracated back over the odontophore, thus pulling food and other particles (Carriker, 1977) into the buccal area for swallowing (Fig. 8). As old teeth are worn down at the distal portion of the radula new teeth are secreted proximally within the radular sac.

The odontophore (Figs. 6,7,8,11) is the supportive base for the radula (Fretter and Graham, 1962) and is reinforced by cartilage. The odontophore and perhaps the radular sheath appear to have associated myoglobin, giving both a dark reddish color.

All snails completely recovered from the anesthesia and were actively moving about the tank within 24 hours post-narcotization. All snails survived until they were sacrificed for examination at the end of the experiment. During narcotization, volume regulation of the drills was apparently hampered; the foot swelled extensively (Fig. 1). The snails recovered from this side effect. It is probable that the drills metabolized small amounts of the Sevin® without any permanent ill effects. The complete radular structure (radula, odontophore, and radular sac) was completely removed from all snails because none of the components were found in the stump of the proboscis.

Within two to five days post-amputation a mass of undifferentiated cells similar to that which Carriker et al. (1972) observed, formed over the stump of the old proboscis. Approximately two weeks post-amputation evidence of proboscis regeneration was observed; a small portion of a new proboscis was formed at the distal end of the old stump. The new proboscis was pale and white due to the absence of myoglobin. This new proboscis increased in length over the following two weeks. Myoglobin first appeared in the proboscis approximately three to four weeks post-amputation. The radula and odontophore of all snails completlely regenerated within four to five weeks post-amputation. Evidence of odontophoral regeneration was observed before radular regeneration occurred (Fig. 7).

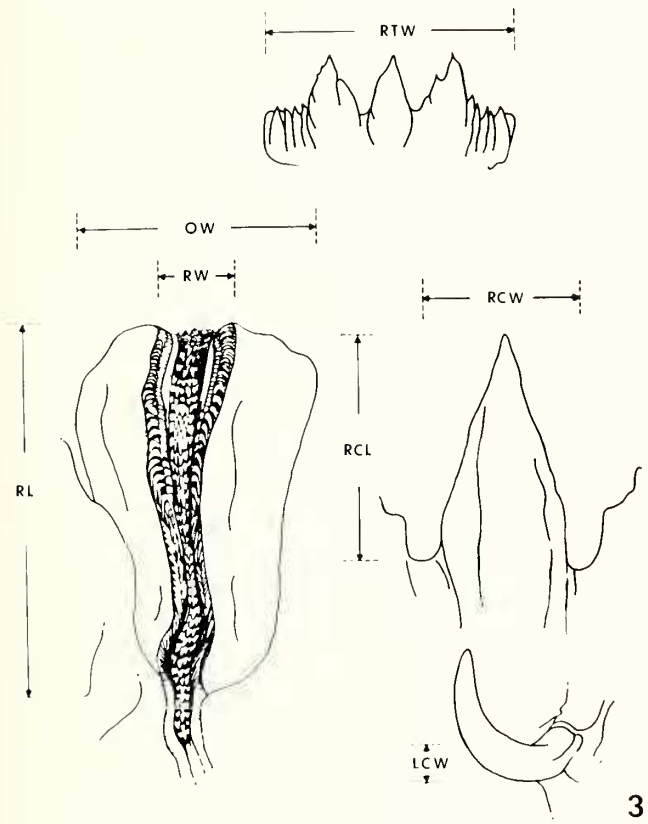


Fig. 3. Measurements of radula and odontophore of *Thais haemostoma canaliculata*: RTW = rachidial tooth width; OW = odontophoral width; RW = radula width; RCW = central rachidial cusp width; RL = radula length (over odontophore); RCL = central rachidial cusp length; LCW = lateral cusp width.

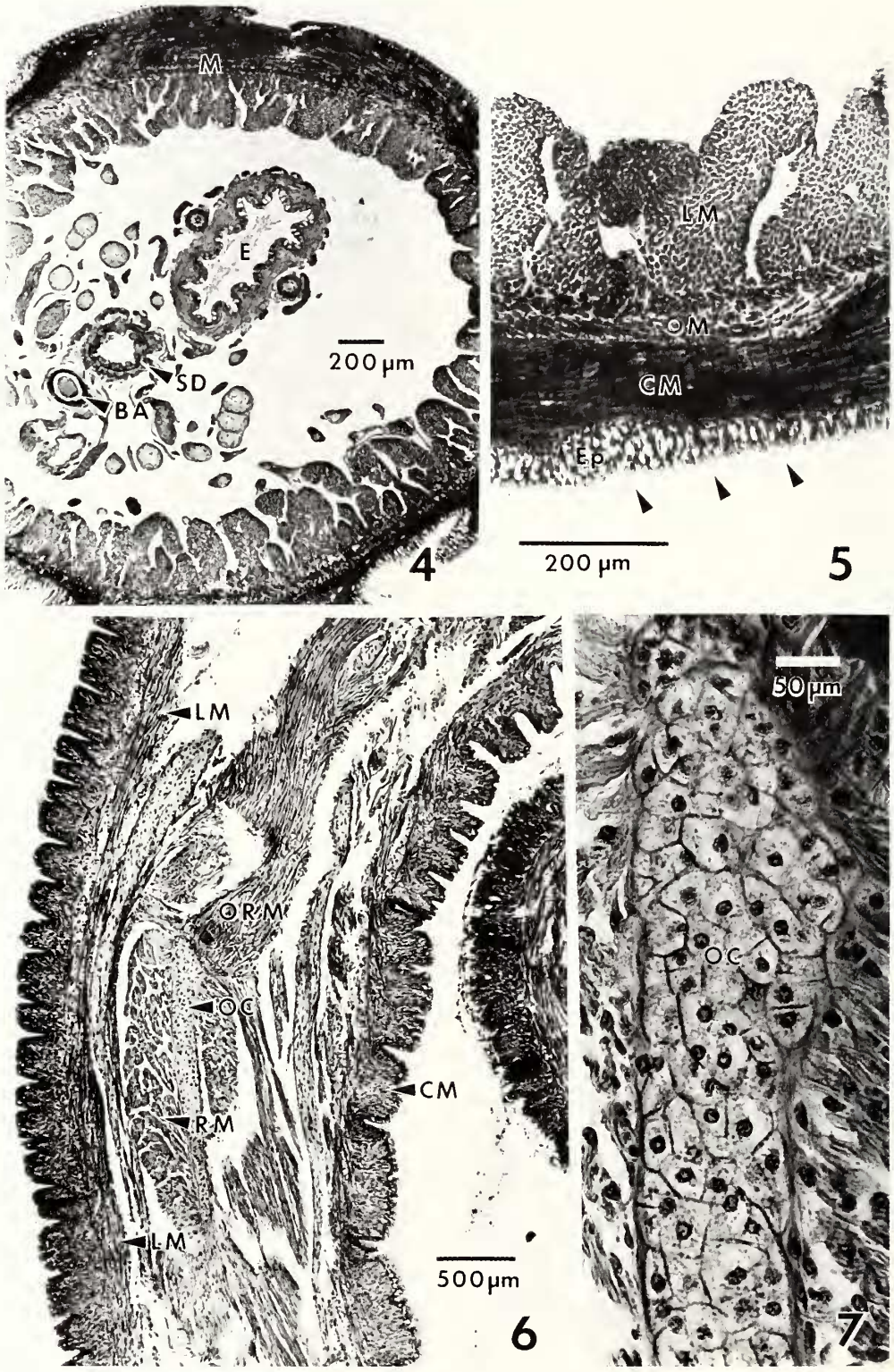


Fig. 4. Cross section of proboscis of *Thais haemastoma canaliculata* proximal to radula: M = muscle layers in proboscis wall; E = esophagus; SD = salivary duct; BA = buccal artery. **Fig. 5.** Cross section of wall of proboscis: LM = longitudinal muscle layer; OM = oblique muscle layer; CM = circular muscle layer; Ep = epithelium. Arrows indicate mucous on epithelium. **Fig. 6.** Longitudinal section of proboscis prior to complete radular regeneration: LM = longitudinal muscle layer; ORM = odontophore retractor muscle; OC = regenerated odontophoral cartilage; CM = circular muscle layer; RM = radular membrane. **Fig. 7.** High magnification of the regenerated odontophoral cartilage (OC) in figure 6.

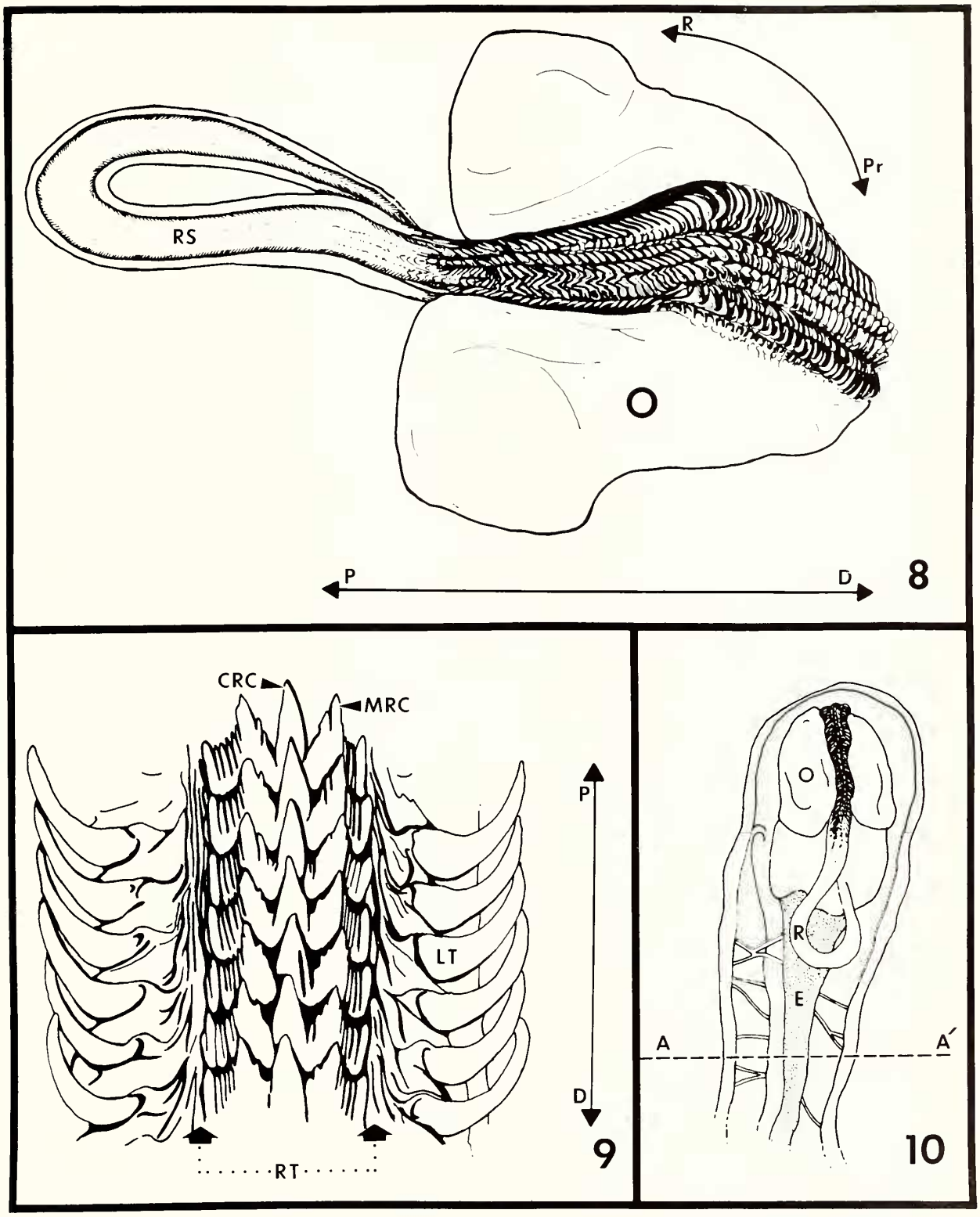


Fig. 8. Diagram illustrating typical radula, odontophore (O), and radular sac (RS) of *Thais haemastoma canaliculata:* R = direction of retraction of radula during drilling; Pr = direction of protrusion of radula during drilling; P = proximal; D = distal; Horizontal field width = 3.5 mm. **Fig. 9.** Drawing of a section of the radula of *Thais haemastoma canaliculata* illustrating the classification and orientation of the teeth: CRC = central rachidial cusp; MRC = marginal rachidial cusp; LT = lateral teeth; RT = rachidial teeth margin; P = proximal; D = distal. Horizontal field width = 550 μm. **Fig. 10.** Diagram of proboscis and contents during amputation: A–A′ = plane of amputation; O = odontophore; R = radular sac; E = esophagus (cut). Horizontal field width = 6.1 mm.

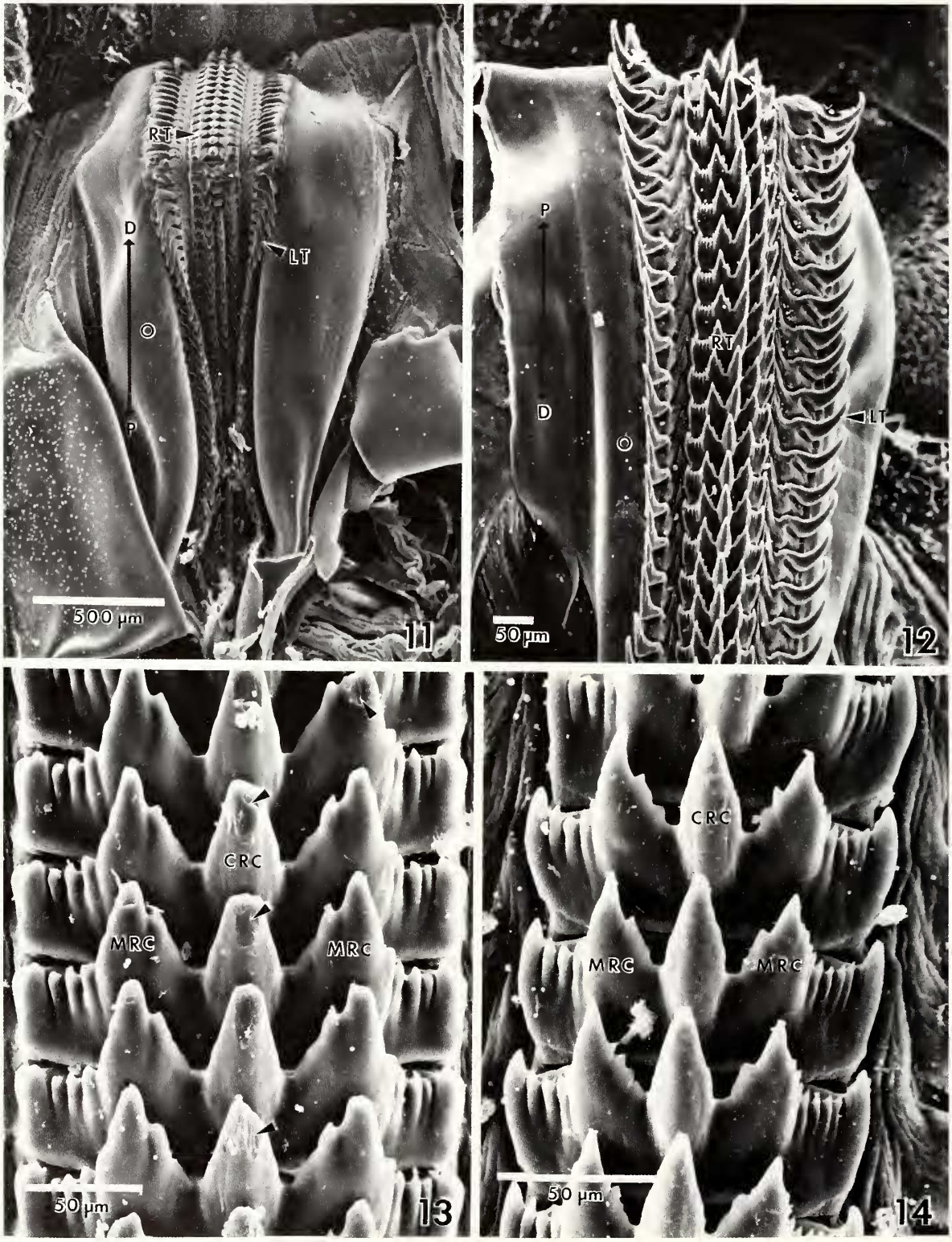


Fig. 11. Original radula and odontophore (O) of oyster drill: RT = rachidial teeth; LT = lateral teeth; D = distal; P = proximal. **Fig. 12.** Regenerated radula and odontophore (4.5 weeks post-amputation) of the same oyster drill in Fig. 11: RT = rachidial teeth; LT = lateral teeth; O = odontophore; P = proximal; D = distal. **Fig. 13.** Rachidial teeth of original radula (Fig. 11): CRC = central rachidial cusps; MRC = marginal rachidial cusps. Arrows indicate wear-marks on cusps. **Fig. 14.** Rachidial teeth of regenerated radula (Fig. 12). Note absence of wear marks on teeth: CRC = central rachidial cusps; MRC = marginal rachidial cusps.

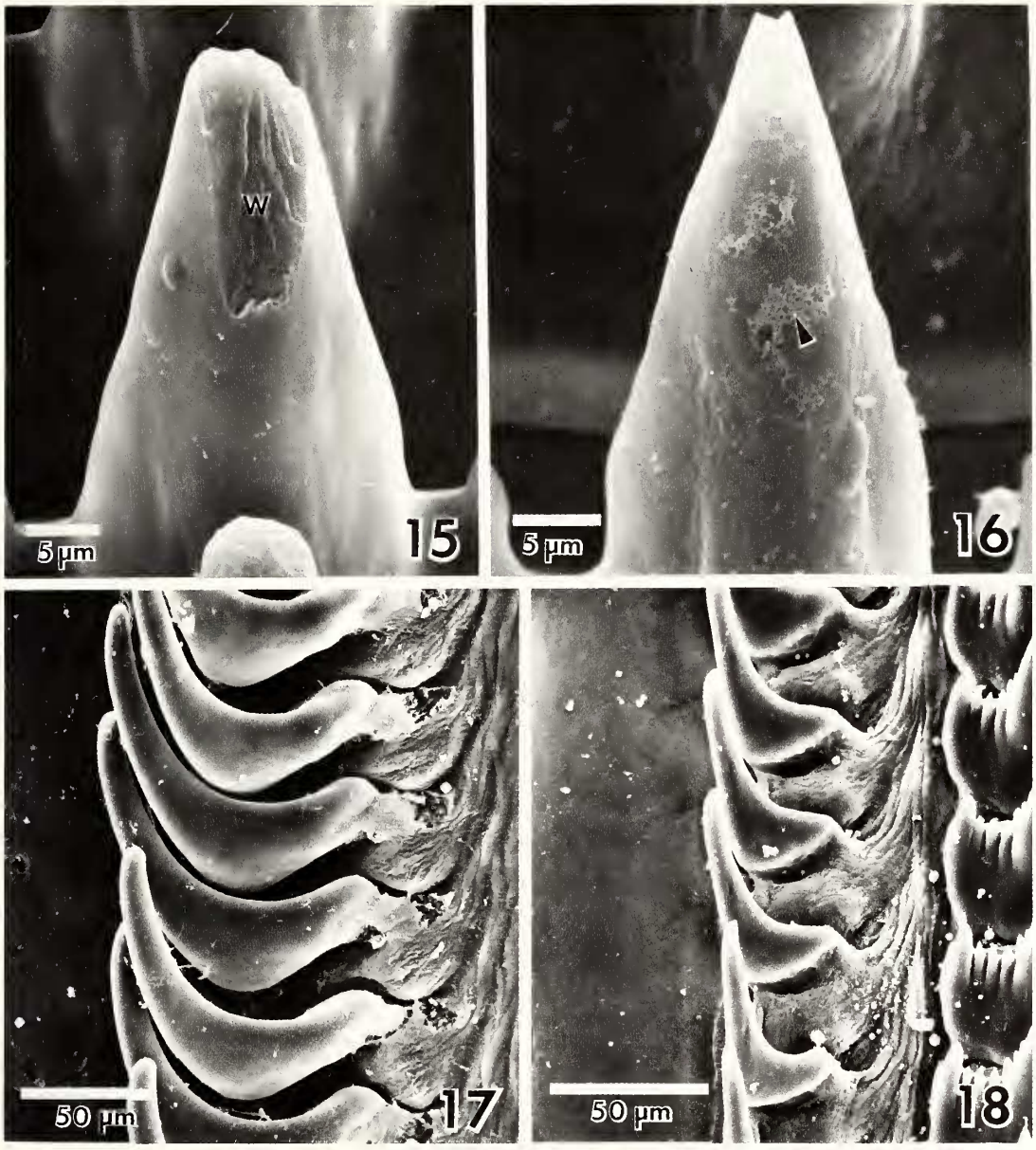


Fig. 15. Original central rachidial cusp of teeth in Fig. 13. W = wear on cusp. **Fig. 16.** Regenerated central rachidial cusp of that in Fig. 14. Arrow indicates mucus on cusp. **Fig. 17.** Lateral teeth of original radula (Fig. 11). **Fig. 18.** Lateral teeth of regenerated radula (Fig. 12).

The regenerated radulae were smaller in size than the original radulae. The size difference is illustrated by SEM micrographs (Figs. 11–18). All regenerated radulae and supportive structures were normal in all respects (Figs. 11–18). No apparent major morphological difference existed between the original and regenerated radulae of any snail with the exception of the amount of wear on the teeth. The original radula of each drill showed more obvious wear on the cusps than the regenerated radula (Figs. 13,14). This wear was especially pronounced on the central rachidial cusps (Figs. 13,15). Size differences between the original and regenerated radulae of the 10 measured snails were observed (Fig. 3). Significant differences ($\alpha = 0.05$) existed between the original and regenerated radulae in radula length, radular width, individual lateral teeth width, central rachidial cusp length, central rachidial cusp width, total rachidial teeth width, and odontophore width (Table 1). No significant difference ($\alpha = 0.05$) existed in the length/width ratio of the central rachidial cusp between original and regenerated teeth.

All 20 snails in tank B resumed feeding within approx-

Table 1. Measurements (μm) of original (O) and regenerated (R) radulae of *Thais haemastoma*. Measurements of regenerated radulae were taken at four weeks post-amputation.

Measurement	O—Radulae	R—Radulae	T Value
Radular Width	406.0 ± 24.50*	274.0 ± 53.70	4.24†
Radular Length	1577.0 ± 70.90	1125.0 ± 57.90	6.67†
Rachidial Teeth Width	153.0 ± 6.33	113.0 ± 5.85	5.51†
Central Rachidial Cusp Length	46.0 ± 6.46	28.1 ± 4.40	5.26†
Central Rachidial Cusp Width	26.0 ± 2.40	16.2 ± 1.96	6.40†
Central Rachidial Cusp Length/Width	1.7 ± 0.15	1.7 ± 0.13	−0.19
Lateral Cusp Width	27.0 ± 2.60	16.3 ± 1.30	3.44†
Odontophore Width	1635.0 ± 88.90	1035.0 ± 87.00	8.08†

*Mean ± S.E.
†Statistically significant at $\alpha = 0.05$.

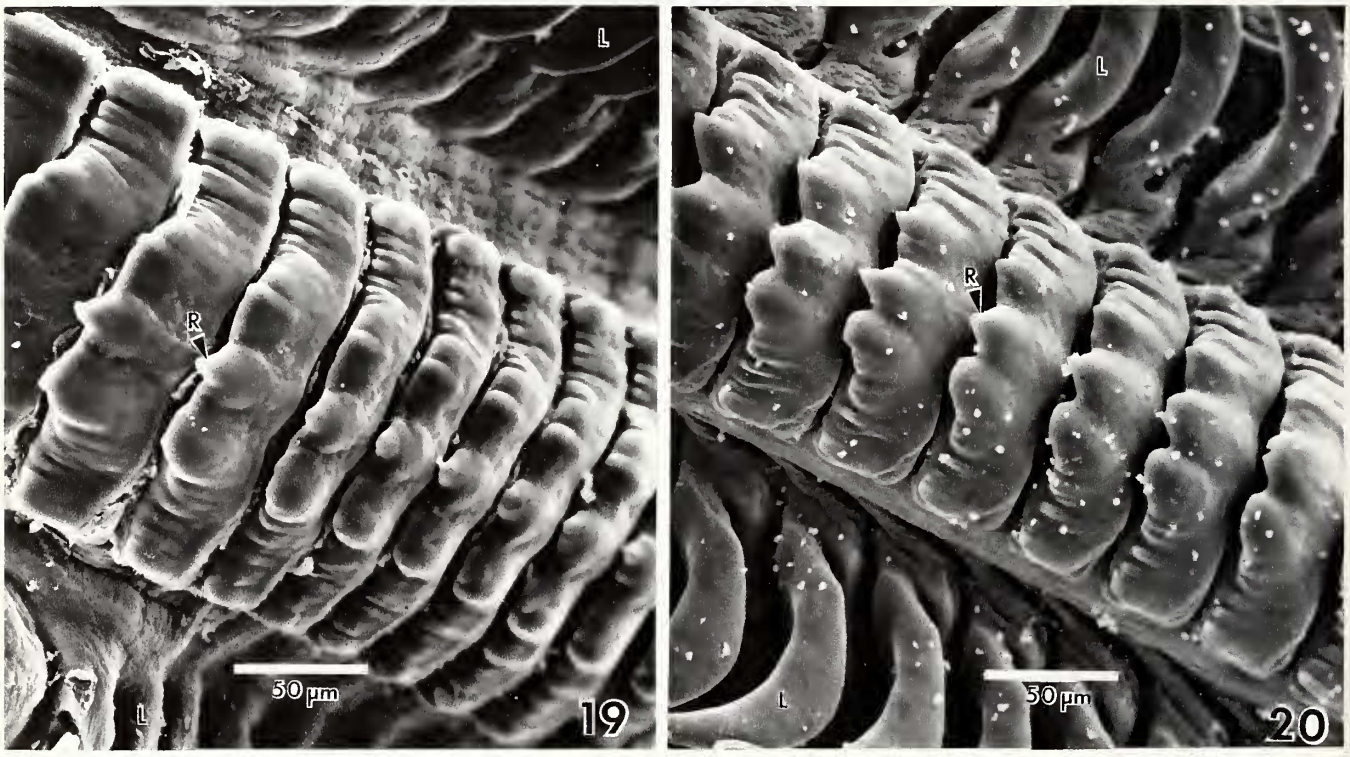


Fig. 19. Original radular anomaly found in one oyster drill: L = lateral teeth; R = reduced central rachidial cusp row. **Fig. 20.** Regenerated radular anomaly of same snail in Fig. 19: L = lateral teeth; R = reduced central cusp row.

imately four weeks (28.8 + 0.28 days) post-amputation. All drills in tank B regenerated a complete, normal-appearing radula, odontophore, and proboscis at the time feeding resumed. No observable differences existed in regeneration time or in the morphological features of the regenerated structures between male and female drills. Likewise, no significant difference (paired t-test; $\alpha = 0.05$) existed in the time to resumption of boring between the two sexes.

An interesting anomaly was seen in the radula of one of the drills examined. The central row of rachidial cusps was much reduced throughout the entire radular length compared to that of the 59 other snails examined (Fig. 19). Originally, we believed that this aberration resulted from wear during drilling and feeding; however, the regenerated radula of the same drill exhibited the same structural malformation (Fig. 20).

DISCUSSION

The southern oyster drill is a euryhaline, estuarine gastropod found along the coasts of the Gulf of Mexico and southeastern United States. It preys primarly on barnacles

and oysters (*C. virginica* and *Ostrea equestris* [Say]) but will also consume the rangia clam (*Rangia cuneata*) in the laboratory. The drill utilizes three organs in the feeding process: the radula, the accessory boring organ, and the hypobranchial gland. The drills use the radula and the accessory boring organ to excavate a hole near the outer margin of the shell of adult oysters. The radula provides the mechanical scraping action to create the borehole; however, the radula is not sufficiently strong to create the hole by itself. Carriker and his associates (Carriker, 1978; Carriker et al., 1978a; and Carriker et al., 1978b) demonstrated that the accessory boring organ in *U. cinerea* produces a chemical secretion that dissolves areas of the outer shell matrix which is then scraped away by the radula. Webb and Saleuddin (1977) observed the borehole formation process in *Nucella* (syn. *Thais*) *lapillus* (Linné) including enzymatic secretions from the accessory boring organ. This appears to be the same drilling pattern that occurs in *T. haemastoma canaliculata*; thus, shell drilling is accomplished by an alternating series of mechanical scraping and chemical dissolution activities. The reader is referred to Carriker (1981) for a complete description concerning the mechanisms of shell penetration and feeding by muricacean and naticacean predatory gastropods.

As mentioned previously *T. haemastoma canaliculata* will usually drill a hole near the ventral margin of the adult oyster shell. Smith (1983) also reported the same bore hole location on adult oysters consumed by *T. haemastoma canaliculata*. We observed that *T. haemastoma canaliculata* will occasionally drill through the central area of the shell and not at the ventral margin when feeding upon oyster spat which have noticeably thinner shells than adult oysters. Snails also drilled through the thick portions of the shell of other individual snails during starvation-induced cannibalism. During cannibalism it is the small snail that is usually eaten. Apparently, *T. haemastoma canaliculata* cannot efficiently drill through the thick central region of adult oysters; therefore, the boreholes are restricted to the thinner outer margin of the adult oyster shell. *Nucella* (syn. *Thais*) *lamellosa* (Gmelin), in contrast, can drill its normal prey, the relatively thin-shelled, blue mussel *Mytilus edulis* Linné (Carefoot, 1977).

During drilling the radula slides over the odontophore and is extended out of the mouth and then retracted back across the substrate (Fig. 8). The drilling process is actually a double action consisting of the odontophore "licking" across the substrate and the radula being drawn back over the odontophore (Carriker, personal communication); thus, the actual effective drilling is accomplished during the retraction stroke. The snail may swallow portions of the shell that are scraped off during retraction. Carriker (1977) provided evidence that *U. cinerea* swallows shell particles rasped off during drilling.

Carriker et al. (1974) analyzed the radular function of *U. cinerea follyensis* Baker by slow-motion photography and scanning electron microscopy. After *T. haemastoma canaliculata* drills a hole in the oyster shell, a paralytic toxin of urocanylcholine (Whittaker, 1960) is released from the hypobranchial gland of the snail into the mantle cavity of the oyster. This toxin paralyzes the oyster's adductor muscle causing the oyster valves to gape. Shell gape allows the snail access between the valves to the soft tissues of the prey. McGraw and Gunter (1972) suggested that perhaps *T. haemastoma* does not need the borehole to feed upon the oyster; instead, the paralytic secretion enters through natural gaps in the margin of the oyster shell causing the oyster to gape. This may have happened in a few instances; however, from the results obtained with the probosectomized snails in tank B, we believe that the proboscis does play an important role in the actual drilling of the shell. The most important point is that the drills need the radular apparatus to ingest the oyster flesh regardless of the method of shell entry. None of the 20 probosectomized snails fed until a complete, functional proboscis and radular mechanism were regenerated, and all oysters that were consumed exhibited boreholes. We often observed several snails feeding on a single large oyster. Smith (1983) found that small oyster drills (1.5–2.5 cm long) produced more boreholes in juvenile oysters than large drills (6.0–7.0 cm long) produced. Smith suggested that small oyster drills may not secrete enough paralytic toxin to cause the oyster valves to gape. It is possible that during predation large oysters require a greater amount of paralytic toxin than one snail is capable of producing. It is probably more advantageous therefore, for several snails to simultaneously attack a large oyster. This may also explain why we usually observed one borehole on small oyster spat and multiple holes on large adult oysters.

Isarankura and Runham (1968) reported on the normal replacement of gastropod radular teeth that are worn during feeding. Our results on *T. haemastoma canaliculata* indicate that radular teeth are progressively worn during the drilling process and must be continuously replaced. The regenerated radula of *T. haemastoma canaliculata* showed no signs of wear (Figs. 12,14,16,18); whereas, the old radula of the same snail showed extensive wear, especially on the central rachidial cusps (Figs. 11,13,15,17). We believe that in *T. haemastoma canaliculata* as in other gastropods (Fretter and Graham, 1962) new teeth are secreted proximally to replace the older, distal radular teeth that are worn down during drilling and feeding.

Carriker et al. (1972) found that regeneration of the proboscis and radular mechanism of *U. cinerea* and *Eupleura caudata* Say was rapid and uniform; resumption of boring varied from 11 to 34 days post-amputation. Their experimental temperature varied between 23.5 and 33.0°C; that variation may explain the wide range of regeneration times. Demoran and Gunter (1956) indicated that *T. haemastoma* could regenerate its proboscis in three weeks after having only the distal portion of the proboscis amputated. Our results agree closely with those of Carriker et al. (1972). We demonstrated that *T. haemastoma canaliculata* can regenerate a complete, fully functional radular mechanism (radula, odontophore, and radular sac) at 23 to 25°C within four to five weeks after complete amputation.

Several factors may account for the differences reported for the regeneration time of the radular mechanism in *T. haemastoma* by Demoran and Gunter (1956) and us. Since Demoran and Gunter (1956) reported that they were able to amputate only the distal portion of the radula, it is quite probable that in their experiment a portion of the regenerative tissue of the radular sac was left behind in the stump of the old proboscis. This is plausible since the radular sac is very long and extends proximally for some distance before curving back toward the odontophore (Figs. 8,10). It is possible that this situation also occurred in the amputation and regeneration experiments of Carriker et al. (1972). In our investigation the method of drill anesthetization permitted complete amputation of the radula, odontophore, and all of the radular sac (Fig. 10). The probosectomized snails in our experiment were able to regenerate a complete radular apparatus from the remaining stump of the original proboscis. The possible presence of a residual piece of the radular sac in the stump of the original proboscis might help to explain the discrepancy between the regeneration time reported for *T. haemastoma* by Demoran and Gunter (1956) and in this study. If a piece of radular sac tissue remained in Demoran and Gunter's snails, then those snails could have regenerated a complete radular mechanism in less time than a drill from which all of the original radular mechanism had been completely removed; hence their three week regeneration time and our four to five week regeneration time are not out-of-line. The use of Sevin® as the anesthetic agent may have slowed the regenerative process of the snails in our investigation; however, the snails recovered so quickly we do not believe that Sevin® alone can explain the difference in regenerative time. Since Demoran and Gunter did not report experimental temperatures, we assumed that it was done at room temperature. Different experimental temperatures might cause differences in regeneration times.

We observed no morphological differences (with the exception of size and wear on the teeth) between the original and regenerated radulae; therefore, it is highly probable that the regenerated radula is normal in both appearance and function. The fact that all 20 snails resumed feeding and drilled normal boreholes in the oyster shells, implies structural and functional normality in the regenerated radula. The further fact that all 20 snails did not feed until the radular mechanism was completely regenerated, demonstrates that the proboscis and radula are necessary for complete predation. The accessory boring organ is not capable of producing a borehole solely by chemical means (Carriker and Van Zandt, 1972; Webb and Saleuddin, 1977), and the snail could not ingest prey flesh without the radular mechanism.

Unlike *N. lamellosa* that feeds directly through the borehole, *T. haemastoma canaliculata* feeds by inserting its proboscis between the valves of the paralyzed oyster. *Thais haemastoma canaliculata*, therefore, runs a higher risk of proboscetomy during feeding than related species such as *N. lamellosa*. It is possible that an oyster may temporarily recover (especially if it is much larger than the snail) from the toxin and close its valves thus injuring and possibly amputating the drill's proboscis and radula. It is also possible that small crabs might inadvertently enjoy the "delicacies" of exposed proboscis flesh once the valves gape and the crabs enter to feast upon the oyster tissue (Carriker, personal communication). In the laboratory we have observed amputation of a *T. haemastoma canaliculata* proboscis where the oyster (*C. virginica*) had apparently recovered from the toxin and closed its valves thus severing the snail's proboscis. It would be advantageous for this species to have evolved a mechanism for replacing the radula that is essential for its survival. Since *T. haemastoma canaliculata* does not normally extend its proboscis fully even when feeding, if an amputation did occur, part of the radular sac would probably be left behind in the remaining stump, possibly reducing the regeneration time.

Carriker (1975) observed a radular anomaly in a *U. cinerea* in which the central rachidial cusp row was missing after the snail was sacrificed. We discovered a similar anomaly in *T. haemastoma canaliculata* (Figs. 19,20) and were able to keep the snail alive until the radula was completely regenerated. The regenerated radula exhibited the same very reduced central rachidial cusp row. As Carriker (1975) pointed out radular anomalies are rare in the Muricidae. This was the only abnormal radula we observed out of several hundred snails examined over the past three years. Carriker (1975) concluded that the loss of the central cusp row could decrease the feeding efficiency of the snail. We agree with this; however, like Carriker we found that the snail was fairly large (shell length = 61.1 mm) and fed successfully on oysters. Since the regenerated radula was malformed and possessed a reduced central rachidial cusp row like the original radula, we believe this anomaly was genetically induced.

In this investigation all of the animals resumed feeding only after the radula was regenerated, and we believe that the times of radular regeneration and feeding resumption are representative of these processes in nature. Since all of the drills in our experiment recovered completely from the Sevin® and exhibited no observable after effects, we believe that this reinforces the use of Sevin® as an appropriate anesthetic agent for these snails. Sevin® permitted full relaxation of the snails and complete amputation of all of the radular mechanism without any of the mortality experienced by Demoran and Gunter (1956).

Our findings and those of Carriker et al. (1972) illustrate that muricid gastropods possess a remarkably adaptive mechanism for regenerating essential structures which could be extensively damaged or amputated in their natural enivonment. This regenerative mechanism has allowed the snail to take advantage of a potentially risky (to the snail) food source: the American oyster *Crassostrea virginica*.

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LITERATURE CITED

Abbott, R. T. 1974. *American Seashells*. 2nd edition. Van Nostrand Reinhold Company, N.Y. 663 pp.

Carefoot, T. 1977. *Pacific Seashores: A Guide To Intertidal Ecology*. University of Washington Press, Seattle, WA. 208 pp.

Carriker, M. R. 1943. On the structure and function of the proboscis in the common oyster drill *Urosalpinx cinerea* Say. *Journal of Morphology* 73:441–506.

Carriker, M. R. 1975. Radular anomaly in *Urosalpinx cinerea* (Gastropoda; Muricidae). *Nautilus* 89(3):91–94.

Carriker, M. R. 1977. Ultrastructural evidence that gastropods swallow shell rasped during hole boring. *Biological Bulletin (Woods Hole)* 152:325–336.

Carriker, M. R. 1978. Ultrastructural analysis of dissolution of shell of the bivalve *Mytlus edulis* by the accessory boring organ of the gastropod *Urosalpinx cinerea*. *Marine Biology (Berlin)* 48:105–134.

Carriker, M. R. 1981. Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. *Malacologia* 20(2):403–422.

Carriker, M. R., and J. W. Blake. 1959. A method for full relaxation of muricids. *Nautilus* 73(1):16–21.

Carriker, M. R., and D. Van Zandt. 1972. Regeneration of the accessory boring organ of muricid gastropods after excision. *Transactions of the American Microscopical Society* 91(4):455–466.

Carriker, M. R., P. Person, R. Libbin, and D. Van Zandt. 1972. Regeneration of the proboscis of muricid gastropods after amputation, with emphasis on the radula and cartilages. *Biological Bulletin (Woods Hole)* 143:317–331.

Carriker, M. R., J. G. Schaadt, and V. Peters. 1974. Analysis by slow-motion picture photography and scanning electron microscopy of radular function in *Urosalpinx cinerea follyensis* (Muricidae; Gastropoda) during shell penetration. *Marine Biology (Berlin)* 25:63–76.

Carriker, M. R., D. Van Zandt, and T. J. Grant. 1978a. Penetration of molluscan and non-molluscan minerals by the boring gastropod *Urosalpinx cinerea*. *Biological Bulletin (Woods Hole)* 155:511–526.

Carriker, M. R., L. G. Williams, and D. Van Zandt. 1978b. Preliminary characterization of the secretion of the accessory boring organ of the shell-penetrating muricid gastropod *Urosalpinx cinerea*. *Malacologia* 17(1):125–142.

Demoran, W. J., and G. Gunter. 1956. Ability of *Thais haemastoma* to regenerate its drilling mechanism. *Science* 123:1126.

Fretter, V., and A. Graham. 1962. *British Prosobranch Molluscs: Their Functional Anatomy and Ecology*. The Ray Society, London. 755 pp.

Humason, G. L. 1972. *Animal Tissue Techniques*. W. H. Freeman and Co., San Francisco, CA. 641 pp.

Isarankura, K., and N. W. Runham. 1968. Studies on the replacement of the gastropod radula. *Malacologia* 7(1):71–91.

McGraw, K. A., and G. Gunter. 1972. Observations on killing of the Virginia oyster by the Gulf oyster borer, *Thais haemastoma*, with evidence for a paralytic secretion. *Proceedings of the National Shellfisheries Association* 62:95–97.

Smith, D. J. 1983. Chemoattraction of the southern oyster drill *Thais haemastoma* toward the oyster *Crassostrea virginica*, as a function of temperature and salinity. *M.S. Thesis, Louisiana State University and Agricultural and Mechanical College*. 84 pp.

Webb, R. S., and A. S. M. Saleuddin. 1977. Role of enzymes in the mechanism of shell penetration by the muricid gastropod *Thais lapillus* (L.). *Canadian Journal of Zoology* 55(11):1846–1857.

Whittaker, V. P. 1960. Pharmacological active choline esters in marine gastropods. *Annals of the New York Academy of Science* 90:695–705.